ORIGIN OF THE MAMMALIA, III. OCCIPITAL CONDYLES OF REPTILIAN TRIPARTITE TYPE.[1]

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THE Huxleyan theory of the origin of Mammalia (Huxley, '80) from primitive Amphibia is still entertained by Howes ('87); it has recently been revived by Hubrecht ('97) upon the basis of the fœtal membranes, and by Kingsley ('99) upon the basis of the homology of the quadrate and upon other grounds. The position taken by the present writer ('98, '99) is that the weight of evidence favors the derivation of the Mammalia from some unknown member of the Anomodont reptiles (Theriodontia) of Permian or lower Triassic age.

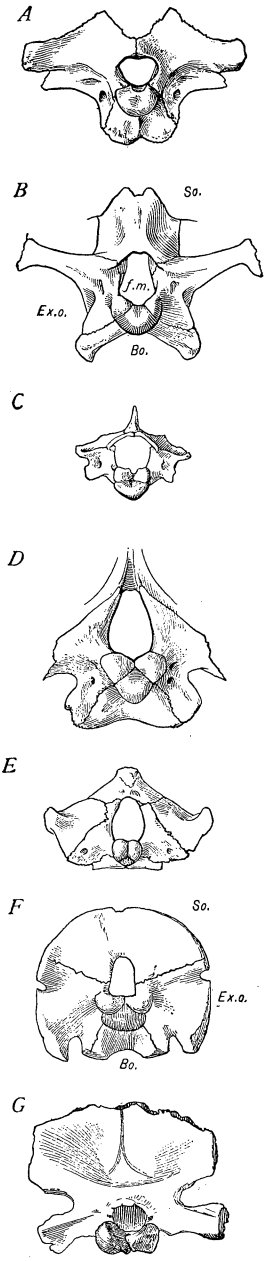
One of Huxley's arguments for amphibian ancestry ('80) was that the paired exoccipital condyles of the mammals were derived from similar amphibian structures. This is cited by Kingsley. The object of the present paper is to show that the *mammalian occipital condyles arose from a reptilian tripartite type by the reduction of the median basioccipital element and the expansion of the lateral exoccipital elements.*

TYPES OF CONDYLES.

The terms "monocondylia" and "dicondylia" employed by Cope fail to express the facts, for the junction of the basal elements of the skull with the atlas vertebra is of four types, — I, II, III, IV, as follows:

I. *Monocondylic, Typical*
Single basioccipital condyle, exoccipitals not entering into articulation . . . . . Reptilia (*e.g.*, Alligator, Ichthyosaurus)

[1] Presented before Section of Zoölogy, American Association for the Advancement of Science, June, 1900. Contributions I and II upon the Origin of Mammals are cited in the bibliography.



II. *Monocondylic, Tripartite.*
Single condyle, basi- and exoccipitals in different proportions.
Reptilia (*e.g.*, Chelone, Fig. 1, *B*, *C*, *D*, *E*).

III. *Dicondylic, Transitional.*
Paired condyles, chiefly exoccipital, partly basioccipital.
Reptilia (*e.g.*, Cynognathus, certain Mammalia).

IV. *Dicondylic, Typical.*
Paired exoccipital condyles, basioccipital element cartilaginous or reduced in median line.
Amphibia (Rana, Mastodonsaurus) and certain Mammalia.

The above types are arranged morphologically, not genetically. Seeley ('88, p. 100) has pointed out the significance of the morphological transition from I to IV as consisting in the reduction of the basioccipital and enlargement of the exoccipital elements; he concludes: "Hence it is possible that the condylar cranial characters may be related in an evolutionary sequence of gradation, and that the change from one condition to another may be consequences of one plan of vertebrate organization rather than that of entirely independent plans."

The diagrams (Fig. 1) have been prepared to illustrate the transition between these types. They show that in the alligator the condyle is wholly basioccipital and below the foramen magnum. In the lizard, python, and two genera of Chelonia we observe a gradual expansion of the exoccipitals and reduction

FIG. 1. — Reptilian condyles. *A*, *Alligator lucius*; *B*, *Iguana tuberculata*; *C*, *Python reticulatus*; *D*, *Chelone midas*; *E*, *Testudo polyphemus*; *F*, Dicynodon (after Lydekker); *G*, Cynognathus (after Seeley). *A–D*, tripartite condyle, typical; *E–G*, reduction of basioccipital element. *Bo.*, basioccipital; *Ex.o.*, exoccipital; *f.m.*, foramen magnum; *So.*, supraoccipital.

of the basioccipital; other Chelonia are typically monocondylic. In like manner certain Anomodontia (Theriodontia) are typically monocondylic; others have a tripartite condyle as figured in Dicynodon (*F*); others again have a tripartite V-shaped condyle with the foramen magnum lying between the exoccipital portions; finally, in Cynognathus (*G*), we have two prominent convex condyles on the lower sides of the foramen magnum composed chiefly of the exoccipitals.

It is from the latter type, in our opinion, that the mammalian structure was probably derived.

But it is first necessary to demonstrate why the apparently obvious derivation of the mammalian from the amphibian condition is improbable.

We do not know the origin of the condyles in the Amphibia; all we know is that as soon as the occipital region becomes osseous, the most primitive amphibians show paired exoccipital condyles with a median cartilaginous or reduced basioccipital element; the reduction of the basioccipital is almost a class character. No Amphibia, so far as known to the writer, exhibit any participation of the basioccipital in the formation of the condyle.

On the contrary, many of the mammals show an extensive participation of the basioccipital in the formation of the condyles; in fact, some mammalian condylar types might

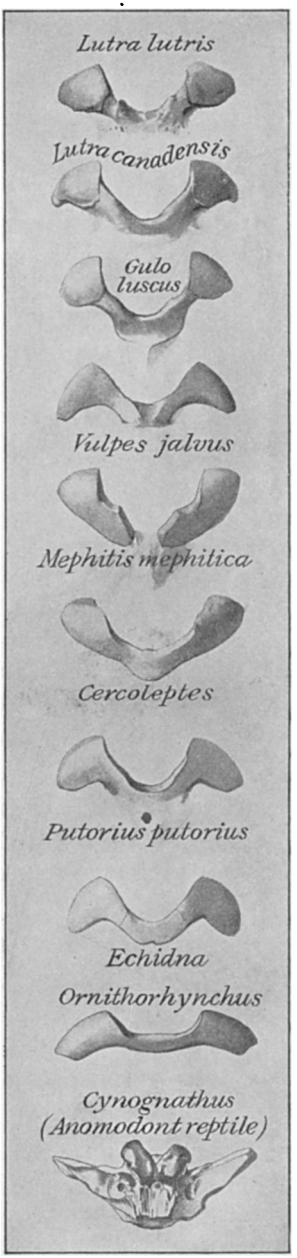


FIG. 2. — Mammalian condyles.

almost be termed tripartite. This gradation between a tripartite or transitional dicondylic condition and the "typical dicondylic" condition in the mammals is very clearly shown in the second series of diagrams (Fig. 2), which show these structures as seen from below or in palatal view.

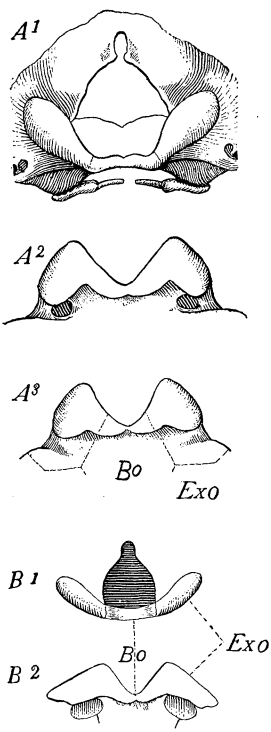


FIG. 3.—A^1–A^2, Echidna (Yale Museum, No. 300): A^1, from behind; A^2, from below; condyles joined by a broad cartilaginous bridge. A^3, Echidna (Yale Museum, No. 1691): from below; condylar surfaces barely separate. B^1–B^2, Ornithorhynchus: condylar ridges continuous; the cartilages are just separate when viewed from behind.

I am indebted to Mr. B. Arthur Bensley, Fellow in Zoölogy, Columbia University, for examining a large series of skulls in the American and Yale Museums (7 Monotremata, 12 Marsupialia, 15 Rodentia, 12 Carnivora, 7 Insectivora, 3 Cheiroptera, 4 Lemuroidea, 3 Anthropoidea, 3 Artiodactyla), with the following results:

Monotremata: The thickness of the basioccipital plates is a conspicuous feature of all monotreme skulls. (Yale Museum, Nos. 244, 300.) In three skulls of Echidna the exoccipital condyles are joined by a broad cartilaginous (basioccipital) bridge, very conspicuous after soaking in water (Fig. 3, A^1, A^2); in two skulls the condyles are joined by a narrow ridge; in two others (A^3) the condylar ridges are discontinuous. In Ornithorhynchus there is little variation in the condylar region (Fig. 3, B^1, B^2); the condylar ridge is continuous across the basioccipital region, the articular cartilages being slightly separate only when viewed from below. So far as this positive evidence goes, it is confirmatory of the theory of tripartite origin.

Marsupialia: The exoccipital condyles are distinct and separate in all forms examined except in Dasyurus, where there is a slight tendency to bridge the basioccipital (*D. maculatus*); this negative result is in keeping with the writer's theory of the *non-primitive* character of the marsupials.

Rodentia: The types examined give negative results.

Carnivora: A more or less distinctly tripartite condition is very common; Lynx, Mephitis, Taxidea, Lutra, Gulo, Putorius, Bassaris (Fig. 2) show all gradations in the participation of the basioccipital.

The conclusions are: (1), unlike reptiles, in no mammal does the basioccipital project backwards as far as the exoccipitals; (2), nevertheless the participation of the basioccipital in the condylar articulation is a common feature, and the monotremes present some grounds for considering it a primitive mammalian feature; (3), the weight of evidence is in favor of derivation from a tripartite type with a depressed basioccipital.

The evolution and gradation of the condyles in the Anomodontia (Theriodontia), from a typically monocondylic to a transitional dicondylic condition, in conformity with other mammalian structures in this order, tend to connect them with the hypothetical ancestral forms of mammals. Taken in connection also with the conditions we have been pointing out among living types, the reptilian tripartite origin of the mammalian condyles is rendered more probable than the amphibian dicondylic origin.

July 20, 1900.

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